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RESEARCH ARTICLE

Streamwise vortices destabilize swimming bluegill sunfish (Lepomis macrochirus)

Anabela Maia1,*, Alex P. Sheltzer2 and Eric D. Tytell2

ABSTRACT

In their natural environment, fish must swim stably through unsteady flows and vortices, including vertical vortices, typically shed by posts in a flow, horizontal cross-flow vortices, often produced by a step or a waterfall in a stream, and streamwise vortices, where the axis of rotation is aligned with the direction of the flow. Streamwise vortices are commonly shed by bluff bodies in streams and by ships’ propellers and axial turbines, but we know little about their effects on fish. Here, we describe how bluegill sunfish use more energy and are destabilized more often in flow with strong streamwise vorticity. The vortices were created inside a sealed flow tank by an array of four turbines with similar diameter to the experimental fish. We measured oxygen consumption for seven sunfish swimming at 1.5 body lengths (BL) s⁻¹ with the turbines rotating at 2 Hz and with the turbines off (control). Simultaneously, we filmed the fish ventrally and recorded the fraction of time spent maneuvering side-to-side and accelerating forward. Separately, we also recorded lateral and ventral video for a combination of swimming speeds (0.5, 1.5 and 2.5 BL s⁻¹) and turbine speeds (0, 1, 2 and 3 Hz), immediately after turning the turbines on and 10 min later to test for accommodation. Bluegill sunfish are negatively affected by streamwise vorticity. Spills (loss of heading), maneuvers and accelerations were more frequent when the turbines were on than in the control treatment. These unsteady behaviors, particularly acceleration, correlated with an increase in oxygen consumption in the vortex flow. Bluegill sunfish are generally fast to recover from roll perturbations and do so by moving their pectoral fins. The frequency of spills decreased after the turbines had run for 10 min, but was still markedly higher in the control, showing that fish partially adapt to streamwise vorticity, but not completely. Coping with streamwise vorticity may be an important energetic cost for stream fishes or migratory fishes.

KEY WORDS: Oxygen consumption, Fish swimming, Respirometry, Turbulence, Kinematics

INTRODUCTION

Swimming is a metabolically costly activity and fish have developed different strategies to reduce energy expenditure (Bone, 1975; Pettersson and Hedenström, 2000). For example, oxygen consumption in fish increases at higher temperature or faster swimming speeds (Claireaux et al., 2006; Fuiman and Batty, 1997; Lee et al., 2003). Less is known about the effects of turbulence and unsteadiness in the flow, in part because turbulence itself is such a complex phenomenon. For example, vortex flows, which are unsteady but not necessarily turbulent, can have vortices with different sizes and intensities, with varying degrees of predictability, or with different orientation (Lacey et al., 2012). Studies of fish behavior in vortex flows have had mixed results. Some fish species are able to take advantage of vertical columnar vortices to decrease metabolic costs, by entrainment and Kármán gaiting (Liao, 2007; Przybilla et al., 2010; Taguchi and Liao, 2011). These studies have focused mostly on vortices shed by horizontal and vertical stationary half-cylinders (Liao, 2007; Taguchi and Liao, 2011; Tritico and Cotol, 2010). Similarly, several groups have found increased fish abundance in areas of streams with high turbulence intensity (Smith et al., 2005; Van Zyll De Jong et al., 1997). Horizontal cylinders, in contrast, destabilize several species of fishes (Eidietis et al., 2002; Webb, 1998; Webb and Cotol, 2010). Finally, other studies have found that generalized turbulence has negative impacts on energetic demands of some fish species (Enders et al., 2003; Lupandin, 2005; Roche et al., 2014; Tritico and Cotol, 2010). Small turbulent eddies may also interfere with sensory receptors (Webb and Cotol, 2010).

Lacey et al. (2012) suggested that some of the diversity in the results could be organized by considering the intensity, periodicity, orientation and size of vortices in a wake, which they termed the ‘IPOS’ (intensity, periodicity, orientation and size) framework. This study fills a gap in the IPOS framework, by considering streamwise vortices, a class of vortex that has received very little attention. Streamwise vortices are shed as part of the ‘horseshoe’ vortex that forms in the wake of a bluff body such as a boulder (Roy et al., 2004; Smith et al., 2005). In fact, because of the boundary layer in streams, any vertical vortices will tend to tilt, becoming more streamwise in orientation. Therefore, this type of turbulence is likely to be very common in streams, and could have a greater impact in lentic freshwater fishes than other turbulent features. This class of turbulence is also commonly generated by boats, hydropower turbines and other propellers. Understanding how different classes of turbulent flows affect fish is essential to mitigate the effects of anthropogenic pressures in freshwater habitats (Lacey et al., 2012). We chose to test the effect of streamwise vorticity on a species whose locomotion has been extensively studied, the bluegill sunfish Lepomis macrochirus Rafinesque 1819. Bluegill sunfish swim with a pectoral fin gait at low swimming speeds, switching to body and caudal fin locomotion at higher speeds (Gibb et al., 1994; Standen and Lauder, 2005; Tytell, 2006). We have data on the contributions of each fin to the wake structure during steady swimming locomotion (Drucker and Lauder, 2001; Tytell, 2006). This species has also been used in studies that examined maneuvering behaviors such as escape responses, maneuvering through complex habitats, braking and accelerating, as well as responses to small hydrodynamic perturbations (Drucker and Lauder, 2001; Ellerby and Gerry, 2011; Flammang and Lauder, 2009, 2013; Higham, 2007; Standen, 2010; Standen and Lauder, 2005; Tytell and Lauder, 2008). The cost of transport for this species has also been shown to

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increase with the gait transition from pectoral fin to caudal fin locomotion (Kendall et al., 2007). However, it seems that fish of this species are not able to produce enough thrust with the pectoral fins alone at higher speeds, thus explaining the costly gait transition (Kendall et al., 2007).

Streamwise vorticity is expected to cause mostly rolling disturbances, while cross-flow, horizontal vortices would cause pitching disturbances and vertical vortices would cause yawing disturbances. Fish have been observed to strongly avoid behaviors that lead to roll (Eidietis et al., 2002). Fish also respond more quickly to roll perturbations, compared with yaw, slip, heave and pitch disturbances (Webb, 2004). We therefore hypothesized that streamwise vorticity would cause a greater increase in oxygen consumption than other orientations of unsteady vortex flows.

In this study, we investigated oxygen consumption and kinematics of bluegill sunfish at various flow speeds and turbine speeds associated with distinct values of streamwise vorticity. Based on our hypothesis, we predicted that the vortices would cause spills and corrections of heading. Oxygen consumption was also expected to increase in the presence of such disturbances. In addition, because higher turbine frequencies will cause higher vortex intensities, resulting in stronger perturbations to the fish, we predicted that higher turbine frequencies would produce stronger corrective reflexes that require more oxygen.

RESULTS
Characterization of the vortices
An array of four small turbines (6 cm diameter) was placed at the upstream end of a flow tunnel (Fig. 1). The turbulence generated by the turbines was characterized using particle image velocimetry (PIV) for the combinations of the three different speeds [0.5, 1.5 and 3.5 body lengths (BL) s⁻¹, based on the average length of the fish] and three turbine frequencies (0, 1, 2 and 3 Hz). Horizontal light sheets indicated that flow was not substantially reduced in the wake of the turbines. To measure the strength of the vortices, flow patterns were measured in a transverse (cross-flow) plane, 10 cm downstream of the turbines, over a period of 3.33 s (1000 frames).

Two of the four vortices were imaged simultaneously. Fig. 2 shows the strength of streamwise vortices for different mean flow speeds and turbine frequencies. The mean circulation for the vortices seen in Fig. 2A over the time period is 106±13 cm² s⁻¹ (mean±s.d.) and the mean radius is 2.2±0.4 cm. No systematic differences were observed among the four vortices. On average, the diameter of the vortices was 100±1% of the body depth of the fish (not including the height of the dorsal or anal fins). The mean peak vorticity (99th percentile) increased with both turbine frequency and flow speed. Circulation increased with increasing turbine frequency, but changed only marginally with increasing flow speed. In contrast, vortex radius decreased at higher flow speeds, but did not change much when turbine frequency changed. At low flow speeds, vortices seemed to be unstable, and would twist around one another. At higher flow speeds, the position was more consistent. Interactions between the four vortices being shed were only observed at low flow speeds.

Kinematics
Streamwise vortices cause bluegill to spill more often and to swim more unsteadily, spending a greater fraction of time accelerating forward or maneuvering from side to side. Spilling events (loss of heading accompanied by head turning, movement downstream and subsequent recovery; Fig. 3A), were virtually absent in control trials, but were common events in unsteady flow (see supplementary material Movies 1 and 2). Spills were more frequent when the turbines were on than in the control treatment at all speeds (Fig. 3A, χ²=30.95, P=0.001). At a swimming speed of 1.5 BL s⁻¹, spill rate increased more than 10-fold from the control (0.3 spills min⁻¹) to the turbines on at 2 Hz (4.5 spills min⁻¹), the same conditions as in our respirometry trials. Bluegill sunfish are generally fast to recover from roll perturbations and do so by moving their pectoral fins simultaneously to produce acceleration. The speed at which the fish were swimming did not affect spill rate (Fig. 3A, χ²=2.135, P=0.344). Individuals did not differ significantly for any of the variables tested (P>0.05 in all cases).

Fish accelerated forward and maneuvered more often when the turbines were running. As shown in Fig. 3B, accelerations were 50% more frequent under the turbulent regime (6% of total swimming time) than in the control (4%, F=8.168, P=0.01). The frequency of maneuvers also increased when the turbines were on (from 5% to 8% of total swimming time, F=14.632, P=0.001, Fig. 3B).

The unsteady movements were also stronger when the turbines were running (Fig. 4). The strength of accelerations, maneuvers and spills was assessed by measuring the average amplitude of any changes in velocity that took longer than one tail beat. We defined accelerations, maneuvers and spills as behaviors that lasted for longer than one tail beat, and thus had frequencies lower than the tail beat frequency. If such movements are present, they will be visible in the low frequency components of the Fourier power spectrum; the higher the average movement amplitude, the larger the low frequency power. For simplicity, we defined low frequency as less than 1 Hz. We estimated the mean amplitude of the behavior by taking the square root of the integral of the signal power at frequencies between 0 and 1 Hz. Accelerations corresponded to the amplitude of forward–back velocity fluctuations, maneuvers to the lateral velocity, and spills to the amplitude of angular velocity fluctuations. At the lowest swimming speed, additional streamwise vorticity increased the strength of accelerations and spills (χ²=7.98, P=0.005).
The presence of turbulence, the mean mass-corrected rate of oxygen consumption (ṀO₂) increased by 18 mg O₂ kg⁻¹ h⁻¹ (0.07 W kg⁻¹) on average compared with the control (t=-2.294, P=0.027, Fig. 6B), but by as much as 58 mg O₂ kg⁻¹ h⁻¹ (0.23 W kg⁻¹) in 25% of cases.

There was a positive correlation between the frequency of accelerations and the rate of oxygen consumption in turbulence (Fig. 7A), but not in the no added turbulence control. Each point in Fig. 7 is from a single trial, with different individuals represented with specific symbols. Four individuals were selected at random for this detailed analysis. Certain individuals were able to compensate for the vorticity better than others, with fewer accelerations and spills, and thus a lower energy cost. Others accelerated a lot, nearly doubling their oxygen consumption. In contrast, the frequency of maneuvers did not affect oxygen consumption in either condition (Fig. 7B).

DISCUSSION

In the wild, fish encounter unsteady flows frequently. In some cases, fish can extract energy from vortices (Liao, 2007; Liao et al., 2003a; Taguchi and Liao, 2011), but in other cases, maintaining heading in unsteady flows increases energy cost (Cotel et al., 2006; Enders et al.,...
drafting, riding the bow wake, or entraining, all strategies that reduce their energy consumption (Liao, 2007). When fish draft or ride the bow wake, they take advantage of the slow flow immediately behind and in front of the cylinder (Taguchi and Liao, 2011; Webb, 1998). When they entrain, they use the shear layer on the edge of the cylinder’s wake to reduce energy consumption (Przybilla et al., 2010; Taguchi and Liao, 2011).

Other studies that examined disorganized turbulence have also found a detrimental effect of turbulence in general. Turbulence reduces critical swimming speed for perch (Perca fluviatilis), particularly when average eddy diameter is close to the size of the fish (Lupandin, 2005). It also increases energy consumption for juvenile Atlantic salmon (Salmo salar) (Enders et al., 2003). Unsteady wave-like motion also increases costs in shiner surfperch (Cymatogaster aggregata) (Roche et al., 2014).

A second reason for increased energy costs in the vortices is that fish must maintain their upright orientation. Streamwise vortices will tend to cause the fish to roll. However, we did not observe any unusually rolling behavior. Maintaining upright posture despite the perturbations from the vortices therefore likely contributes to the increased energy cost. Indeed, we often observed unusual, unilateral pectoral fin use (see supplementary material Movie 3), indicating that the fish must coordinate their fins in unusual, and possibly energetically costly ways to maintain upright posture.

We saw few substantial differences in the effects of the vortices as we increased the turbine speed (Figs 3 and 4). This lack of difference may be a consequence of the turbine design; circulation and vortex radius did not change much as we increased the turbine speed (Fig. 2). It may be that the turbines had too many blades. As rotation speed increased, they may not have been able to entrain enough fluid to impart additional rotational momentum.

Although our study showed that streamwise vorticity increases swimming costs in a similar way to that found in other studies

![Fig. 5. Spill rate decreased after 10 min of accommodation.](image)

<table>
<thead>
<tr>
<th>Control</th>
<th>0 min</th>
<th>10 min</th>
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<tr>
<td>0</td>
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![Fig. 6. Oxygen consumption under turbulent and control flows.](image)

A) Representative traces of different trials for the same individual showing raw oxygen concentration data fitted with linear regressions with the turbines off (0 Hz frequency, open squares) or on (2 Hz frequency, red circles). $M_o$, mass-corrected rate of oxygen consumption.

B) Mass-corrected oxygen consumption standardized by the control mean for each fish separately. Bars represent 25th and 75th percentiles.
relationship is with accelerations under turbulence, shown with a red line in A. The shaded region in A represents the standard error in the estimate of the slope.

(B) with turbines off (0 Hz frequency, open symbols) and running at 2 Hz (red symbols). Different symbols represent different individuals. The only significant effect was with accelerations under turbulence, shown with a red line in A. The shaded region in A represents the standard error in the estimate of the slope.

We hypothesized that streamwise vorticity might be more detrimental to fish than horizontal or vertical vortices. Instead, our results suggest that streamwise vortices may have a relatively small impact on bluegill sunfish. The vortices were probably large enough to cause an effect on the fish, because they were the same diameter on average as the fish’s body depth, not including the depth of the dorsal and anal fin. Increasing the vortex size so that the vortices were the same diameter as the body and fin depth could cause a larger effect. Several studies have found that vortices with diameters less than about 30% of the fish’s size have no effect, and that large effects were not observed until the vortices reached 75% of the fish’s size (reviewed in Lacey et al., 2012).

Another possibility is that the streamwise orientation of the vortices may limit their impact. Horizontal cross-flow vortices or vertical vortices are shed periodically (Lacey et al., 2012). Thus, their effects may be different in time and position along a fish’s body, as the vortices move downstream. Streamwise vortices, in contrast, should have effects that are similar all along a fish’s body. Because fish generate force by accelerating fluid along their bodies, the differential effects of horizontal and vertical vortices may interfere more with the physical processes that fish use for generating thrust. Flow visualization will be necessary to understand exactly how fish are interacting with the vortices.

Individual fish also differ substantially in their ability to compensate for the vortices (Fig. 7). Some fish accelerate relatively little (Fig. 7A), and do not require much more energy than in the control case, while others accelerate a lot and use dramatically more energy (see outlier point in Fig. 6B, which corresponds to a fish that used 82% more energy in the vortices). All fish also learned to compensate better, although not completely, over time (Fig. 5). The differences in compensation and learning may be related to the unusual asynchronous fin motion that we often observed (supplementary material Movie 3). Perch subjected to comparable sized vortices also use asynchronous fin motion (Lupandin, 2005). Asynchronous fin movement has been shown to be used by a variety of fish while maneuvering (Bartol et al., 2003; Standen, 2010; Webb, 2006).

Streamwise vorticity occurs in the wild both from anthropogenic pressures such as boats, energy turbines and other propellers and naturally from river confluences, meandering and interactions with obstacles in the river bed (Harrison et al., 2011; Roy et al., 2004; Smith et al., 2005). In the wild, streamwise vorticity might be more detrimental as it is not frequently constant or predictable. The metabolic costs we observed may be amplified in wild populations as wild fish may not be able to acclimate to constant vorticity like fish in the laboratory did (Fig. 5).

Conclusions

Fish must use more energy to swim in flow with streamwise vortices, which are shed off both rough elements on a streambed (Roy et al., 2004) and man-made devices like turbines and propellers (Whale et al., 2000), likely because they swim less steadily and move their pectoral fins in an unusual asymmetric way. The additional energy required is relatively low on average (6% over baseline swimming costs), but can be dramatically higher for certain individuals (up to an 82% increase). Some individuals swim more steadily in the vortices, using less energy, probably because they learned better how to compensate for the vortices; others swim less steadily and used more energy. Future work must examine how prevalent such vortices are naturally and how the effects change as the size of the vortices changes, so that we can better understand the role of vorticity and turbulence in the energy budget of fish in nature.

MATERIALS AND METHODS

Animals

Seven bluegill sunfish, *L. macrochirus*, were captured by beach seine in White Pond, Concord, MA, USA. The bluegill were housed individually in 10 gallon tanks at 19.5°C with pH 7.4 and fed live worms daily. Lights were kept on a day–night cycle that matched the time of year. The same animals were used first in the respirometry experiments and then in the kinematics experiments, with at least 1 week interval between. Fish body length (BL) ranged from 12.5 to 15.1 cm (mean ± s.d.=13.3±1.0 cm,) and mass ranged from 45.1 to 65.2 g (55.6±8.6 cm). Fish body depth (dorsalventral, not including dorsal or anal fin depth) was 0.34±0.01 BL (4.4±0.1 cm) and width was 0.14±0.01 BL (1.8±0.2 cm). Husbandry and experiments complied with federal animal care and use standards and were approved by the Tufts University Institutional Animal Care and Use Committee.

Characterization of the vorticity

Four custom-designed turbines were printed in ABS plastic using a 3D printer (Stratasys Dimension 1200, Stratasys, Eden Prairie, MN, USA). The turbines...
had a diameter of 6 cm with a blade length of 5 cm. We chose turbines of this size so that the vortices generated would be similar in diameter to the depth of the fish. Each turbine was spaced 2 cm from the surrounding turbines, blade to blade, 5 cm away from the tank walls (Fig. 1). The set of four turbines was placed at the upstream end of the working section of a flow tunnel (25×26×150 cm). PIV was used to characterize the turbulence generated by the turbines (Tytell, 2010). A continuous diode laser (Opus model, 5 W; Laser Quantum, Cheshire, UK) was used at 4 W together with optics to create transverse and horizontal sheets to characterize the turbulence shed by the turbines spinning at 1, 2 and 3 Hz with background flows of 0.5, 1.5 and 2.5 BL s⁻¹ (based on average bluegill sunfish length). Horizontal sheets were placed at the mid-turbine blade, the blade center and in between the turbines. The transverse sheet was placed across the flow, 10 cm behind the turbines, which was the area where fish spent most of their time. A Phantom Miro M120 (Vision Research, Wayne, NJ, USA) was used to gather high speed video at 500 frames s⁻¹ and PIV data were analyzed using Insight 4.1 (TSI Inc., Shoreview, MN, USA). The camera was placed downstream of the light sheet at ~30 deg angle to the flow. A full-field calibration was performed to correct distortion (‘Off-axis PIV’; TSI Insight). To quantify the strength of the vortices, vortex centers were identified manually and circulation Γ was calculated, using the following equation: Γ = Ω dl, where Ω is the velocity vector and dl is the tangent vector along the circular contour S (Tytell, 2010). Circulation was calculated in contours of increasing radius until a maximum circulation value was reached; the vortex radius is the one with the maximum circulation. The 99th percentile of counter-clockwise vorticity was also calculated, as an estimate of the peak vorticity. Mean circulation, peak vorticity and vortex radius were calculated by averaging across 10 frames, taken every 0.5 s.

Respirometry
Fish were starved for 48 h before respirometry trials to account for specific dynamic action (Beamish, 1974). The fish were weighed and measured, then placed in a 29 l recirculating flow tank respirometer (Logolos Systems, Tjle, Denmark), equipped with a Pro Odo dissolved oxygen probe (YSI, Yellow Springs, OH, USA). The temperature in the tank was maintained between 19.5 and 20.5°C. The fish were confined to a 30 cm long section of the 25×26×150 cm (height×width×length) working section. For respirometry experiments, a DRS Lighting High-Speed RDTI camera (DRS Technologies, Parsippany, NJ, USA) was used at 25 frames s⁻¹ to capture a ventral view. In order to sample kinematics consistently over the entire duration, 6 s of video were recorded to disk for each 20 s of experimentation. For each individual fish, three trials were performed for each of two conditions: no turbulence, right after turning the turbines on and after 2 Hz; t-tests were also used to compare the frequency of maneuvers and accelerations during control and turbulence conditions. Linear regressions were also used to determine the relationships between $\dot{M}_{O_2}$ and frequency of accelerations and maneuvers. Frequency of spills, accelerations and yaw maneuvers were tested against turbine frequency (0, 1, 2 and 3 Hz), flow speed (0.5, 1.5 or 2.5 BL s⁻¹) and individual with ANOVA when the data were normally distributed and with a Kruskal–Wallis test when the assumptions could not be met. Adaptation to the turbines was also tested using Kruskal–Wallis to compare spill frequency in the three conditions: no turbulence, right after turning the turbines on and after 10 min. Statistical tests were performed using JMP software (SAS, Cary, NC, USA). Values reported are means and s.d., unless indicated otherwise.

Acknowledgements
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Competing interests
The authors declare no competing or financial interests.

Author contributions
A.M. designed the experiments, conducted all experiments, coordinated the data analysis and estimate derivatives (following Walker, 1998). We defined accelerations, maneuvers and spills as behaviors that took longer than one tail beat. To quantify the amplitude of the behaviors, we arbitrarily set a cut-off at 1 Hz and analyzed the low frequency portion (0 ≤ f ≤ 1 Hz) of the power spectra of the forward velocity, lateral velocity and body angular velocity. The intensity of each type of behavior was estimated by taking the square root of the integral of the power spectra over this frequency range.

Statistical analysis
To analyze the effect of the turbines on the rate of oxygen consumption, an ANOVA test was performed with turbine frequency and fish as the independent variable and normalized $\dot{M}_{O_2}$ as the dependent variable. As no individual effects were observed, a t-test was used to compare the control and vortex flows at 2 Hz; t-tests were also used to compare the frequency of maneuvers and accelerations during control and turbulence conditions. Linear regressions were also used to determine the relationships between $\dot{M}_{O_2}$ and frequency of accelerations and maneuvers. Frequency of spills, accelerations and yaw maneuvers were tested against turbine frequency (0, 1, 2 or 3 Hz), flow speed (0.5, 1.5 or 2.5 BL s⁻¹) and individual with ANOVA when the data were normally distributed and with a Kruskal–Wallis test when the assumptions could not be met. Adaptation to the turbines was also tested using Kruskal–Wallis to compare spill frequency in the three conditions: no turbulence, right after turning the turbines on and after 10 min. Statistical tests were performed using JMP software (SAS, Cary, NC, USA). Values reported are means and s.d., unless indicated otherwise.

Supplementary material
Supplementary material available online at http://jeb.biologists.org/lookup/suppl?doi=10.1242/jeb.114363/-/DC1

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